

COMPREHENSIVE REVIEW



## Circadian rhythmicity of body temperature and metabolism

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### ABSTRACT

This article reviews the literature on the circadian rhythms of body temperature and whole-organism metabolism. The two rhythms are first described separately, each description preceded by a review of research methods. Both rhythms are generated endogenously but can be affected by exogenous factors. The relationship between the two rhythms is discussed next. In endothermic animals, modulation of metabolic activity can affect body temperature, but the rhythm of body temperature is not a mere side effect of the rhythm of metabolic thermogenesis associated with general activity. The circadian system modulates metabolic heat production to generate the body temperature rhythm, which challenges homeothermy but does not abolish it. Individual cells do not regulate their own temperature, but the relationship between circadian rhythms and metabolism at the cellular level is also discussed. Metabolism is both an output of and an input to the circadian clock, meaning that circadian rhythmicity and metabolism are intertwined in the cell.

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## Introduction

The award of the 2017 Nobel Prize in physiology to three researchers who first identified the molecular mechanism of circadian rhythms helped bring the attention of life scientists and health professionals to the importance of circadian rhythmicity for the healthy operation of living organisms [1,2]. Disruption of the relationship between the internal circadian clock and the synchronizing environmental cycle (such as the disruption observed after transcontinental travel, during shift work, or even concomitantly with the extensive use of artificial light in the modern 24-hour society) has been shown to have serious negative health effects, including breast cancer, cardiovascular disease, psychiatric disorders, and the metabolic syndrome [3–7].

One of the first physiological variables subjected to long-term monitoring that allowed the determination of daily rhythmicity in the mid 1800's was body temperature [8,9]. Studying the rhythmicity of body temperature is important for at least two reasons: 1) the body temperature rhythm is a convenient marker of the circadian clock for studies on biological rhythms and sleep, and 2) the rhythm interacts with a concurrent rhythm of

metabolism and reflects a constant conflict between homeostasis and circadian rhythmicity in the control of core temperature in mammals and birds. Two previous comprehensive literature reviews were published 28 years ago [10] and 10 years ago [11]. Reviews by other authors have concentrated on particular aspects of the rhythmicity of body temperature [12–14].

Unlike mammals and birds, most living beings on Earth (including fungi, plants, microbes, and the majority of animal species) do not regulate the temperature of their bodies by autonomic mechanisms [15,16]. This means that, in the absence of effective behavioral adjustments (which are also limited to a few taxonomic groups), the body temperature of an organism will vary with the temperature of the environment. Because of the dependence of biochemical reactions on temperature, this means also that the organism's metabolism will vary with the temperature of the environment. It is not surprising, therefore, that the body temperature and metabolism of most living beings on Earth will oscillate daily and seasonally along with the daily and seasonal oscillation in environmental temperature. However, a relatively small group of animals (primarily mammals and birds) regulates body temperature by both behavioral and autonomic mechanisms [17–19]. These

animals, often called endothermic homeotherms, can maintain a relatively stable body temperature while exposed to heat or cold because of their ability to modulate metabolic heat production as well as convective and evaporative heat loss. As emphasized by Claude Bernard in the 19th century, the constancy of physico-chemical properties of the internal environment of an organism is essential for a free life [20]. Yet, as will be discussed here, body temperature and metabolism exhibit daily and seasonal variation in mammals and birds – not as a direct effect of variation in ambient temperature but as an endogenously controlled process. An endogenously generated physiological oscillation with a period (duration) of approximately 24 hours is called a circadian rhythm [21], and this article will deal with the circadian rhythmicity of body temperature and metabolism. Seasonal oscillation in body temperature and metabolism (as reflected principally in the process of hibernation) has been reviewed by others recently [22,23] and will not be covered here. This review will concentrate on circadian rhythmicity.

## Circadian rhythmicity of body temperature

### Research methodology

A first requirement for the recording of circadian rhythms of body temperature is the possession of a thermometer. Although a standard clinical thermometer can be used if the animals are not disturbed by the frequent contact with the experimenter, more sophisticated thermometers are required for measurements taken many times a day for many consecutive days. The monitoring of body temperature in human subjects can be easily accomplished with commercially available biomonitors systems such as those marketed by AD Instruments Inc. (Colorado Springs, Colorado), Biopac Systems Inc. (Goleta, California), Mindware Technologies Ltd. (Gahanna, Ohio), and Noldus Information Technology (Wageningen, Netherlands). Temperature-sensitive radio transmitters may be conveniently swallowed [24,25], although they stay in the digestive system for only a few days and are of limited use in long-term studies. Gut temperature measured with a swallowed sensor-transmitter correlates better with rectal temperature than does axillary temperature (measured under the arm) [26].

Monitoring of body temperature in other animal species usually involves surgically implanted temperature-sensitive sensors for short-range telemetry in the laboratory [27–32] or surgically implanted data loggers for free-ranging animals [33–38] (see also Table 1 in the review article by Maloney and colleagues [14]). For telemetry equipment, the major manufacturers in the United States are Data Sciences Inc. (St. Paul, Minnesota), the Stellar Telemetry branch of TSE Systems (Chesterfield, Missouri), the Implantable Telemetry branch of Millar Inc. (Houston, Texas), and the E-Mitter Telemetry branch of Starr Life Sciences (Oakmont, Pennsylvania). Starr Life's E-mitters and Millar's Telemeters are transponder transmitters (that is, transmitters that are tele-energized by the radio receiver). This feature is especially convenient in long-term studies in which traditional transmitters will run out of battery, although transponder transmitters require maintenance after one or two years of operation, which reduces their advantage over battery-based transmitters in multi-year studies.

An alternative to telemetry, especially for field studies, is the data logger. Data loggers are devices that can record and store data. The advantage over telemetry is that the experimental subjects can move freely over large distances without causing a loss of signal. A disadvantage is that the experimenter cannot access the data until the logger is retrieved. Manufacturers of data loggers include DataTaker Ltd. (Rowville, Australia), Onset Computer Corp. (Bourne, Massachusetts), and Pico Technology Ltd. (St. Neots, United Kingdom). A very convenient data logger is the iButton temperature logger (Maxim Integrated Products, San Jose, California). These

**Table 1.** Studies documenting the existence of daily rhythmicity of body temperature.

Laboratory rats	[30,39–87,308,385,386,396,428,429,611,629,642,645]
Domestic mice	[31,88–116,424]
Golden hamsters	[117–123,310,628,631,648]
Other rodents	[28,32,35,124–166,306,346,374,380,446,450,454,562,577,651,652]
Dogs and cats	[167–176]
Goats and sheep	[177–187,314,372,381,433,434]
Horses and bovines	[33,188–198,315,322]
Non-human primates	[199–217,378,387,431,432,469,610]
Humans	[9,26,218–261,520,622,623,627]
Other mammals	[27,29,38,262–286,342,370,371,373,375–377,412,453]
Birds	[36,287–303,382,395,414,415]

miniature loggers (16-mm diameter) can be surgically implanted like radio transmitters. Like larger loggers, iButtons have the advantage of not requiring a separate receiver and the disadvantage of not allowing on-line access to the data. Memory limitations make them unsuitable for long studies with high temporal resolution. Available at a higher price but having the ability to record data for much longer are the miniature data loggers marketed by SubCue Dataloggers (Calgary, Canada) and Star-Oddi Ltd. (Gardabaer, Iceland).

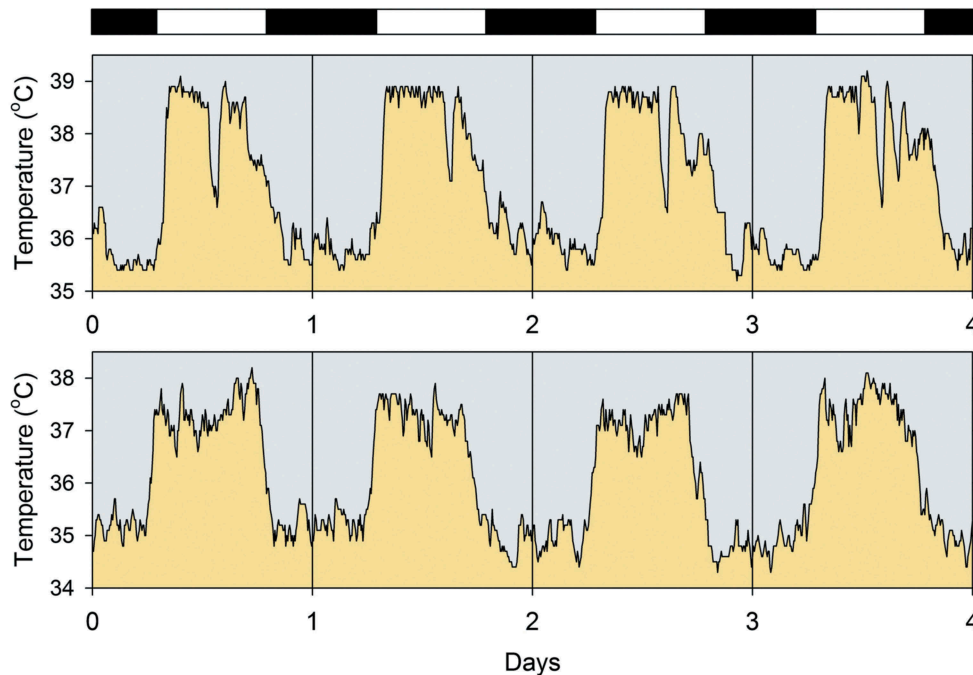
In large animals, surgical implantation can be avoided. TekVet Technologies (Garden City, Kansas) and FeverTags (Amarillo, Texas) manufacture temperature transmitters for use in livestock. The transmitters are placed in the animal's ear, close to the tympanic membrane, thus allowing measurement of core temperature without the need for surgical intervention. This technology has not been thoroughly evaluated in livestock, and evaluations with human subjects have not been very encouraging [304,305]. For smaller animals in a laboratory setting, including small rodents, temperature-sensitive PIT tags (passive integrated transponder radio-frequency identification devices) can be used [306]. The tags are the size of a grain of rice and can be injected with a syringe

subcutaneously or intraperitoneally without the need for a surgical procedure. Because they are transponders, PIT tags require no batteries and can be used uninterrupted for years. Biomark Inc. (Boise, Idaho) is a major supplier of PIT tag equipment.

### Endogenous determinants

Daily rhythmicity of body temperature has been extensively documented in many species of birds and mammals. More than 300 articles are listed in Table 1. Although the studies varied greatly in methodology and experimental design, they all provided evidence of a regular daily oscillation of body temperature in a variety of species.

An example of the daily rhythm of body temperature is shown in Figure 1. The data were obtained from two white-tailed antelope squirrels (*Ammospermophilus leucurus*) individually housed in the laboratory [306]. The body core temperature of both animals rose daily at the time of lights-on and declined to a nighttime low shortly after lights-off. One of the squirrels (top panel) exhibited a brief temperature decline in the middle of the light phase, whereas the other squirrel (bottom panel) did not. The mean and range of oscillation



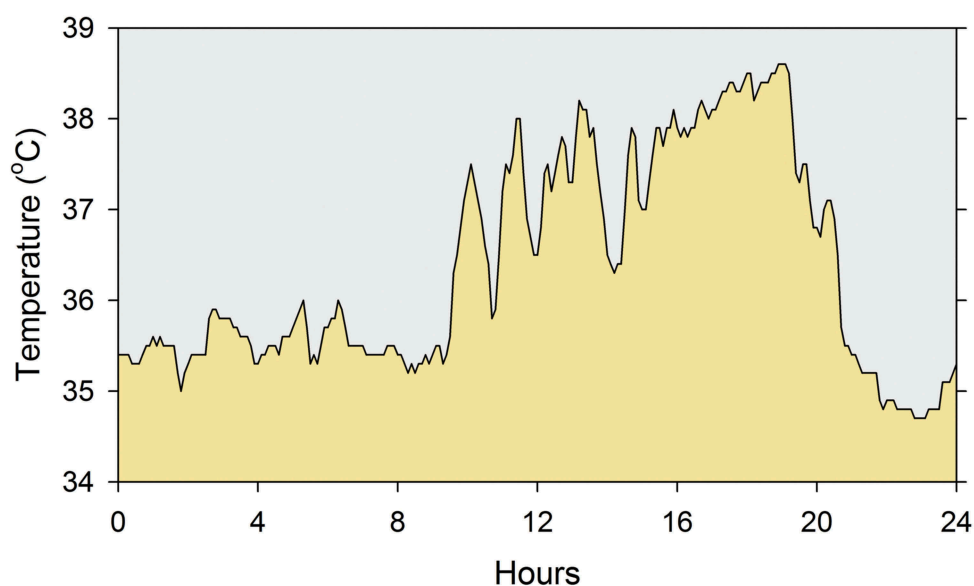
**Figure 1.** Four-day segments of the records of body temperature of two white-tailed antelope squirrels (*Ammospermophilus leucurus*, 120 g average body mass) housed individually in the laboratory at 25°C. The data were collected and are plotted with 6-minute resolution. The white and black bars at the top indicate the light and dark phases of the prevailing light-dark cycle.

of the rhythms of the two animals were similar but not identical.

The records of body temperature of another white-tailed antelope squirrel are shown in greater temporal resolution in [Figure 2](#) so that high-frequency oscillations can be seen better. Superimposed on the daily oscillation, one can see somewhat irregular oscillations, with smaller amplitude, lasting approximately 1 or 2 hours. Such ultradian oscillations in body temperature have received much less attention from researchers than circadian oscillations [307], but they have been noted in reports of the rhythmicity of body temperature in rats [308,309], golden hamsters [310,311], lemmings [312], squirrel monkeys [313], sheep [314], and dairy cows [315]. Whereas the circadian rhythmicity of body temperature has been thoroughly confirmed by formal time series analysis [316–319], ultradian rhythmicity has rarely been formally analyzed. Nonetheless, spectral analysis of body temperature data from rats and hamsters has been conducted and has documented statistically significant ultradian oscillation, predominantly in the range of 2 to 12 hours [308–311]. Still unsettled is the question of whether the high-frequency peaks in the periodograms represent true biological rhythms or merely the harmonics needed to describe the waveform of a circadian rhythm generated by a pacemaker that does not produce an ideal sinusoidal signal. As a matter of fact, the shape (waveform) of the circadian

rhythm of body temperature has not been thoroughly studied. The waveform is generally described as sinusoidal, although it is often bimodal or square, and there have been very few attempts to quantify the description of the waveform of circadian rhythms. The strength (robustness) of circadian rhythms, which is related to the stability of waveform, has received a little more attention [320], but very little is known about the determinants of the waveform of circadian rhythms. As for ultradian oscillations, it has even been argued that they should be called “episodic ultradian events” (and not “ultradian rhythms”) because the oscillations are most often aperiodic [321].

For investigation of the characteristics of endogenously-generated rhythms, organisms must be studied in non-rhythmic environments. Although researchers have not always made certain that environmental conditions were exactly constant, many laboratory studies have ensured the absence of cycles of ambient temperature, food availability, and predator danger. For standardization purposes, most studies maintained a light-dark cycle with 12 hours of light and 12 hour of darkness per day. Data from 218 studies with 93 species are summarized in [Table 2](#). It can be seen that the main parameters of the body temperature rhythm – mean, range of oscillation, and acrophase (peak time expressed in hours after lights-on) – vary somewhat



**Figure 2.** One day segment of the records of body temperature of a white-tailed antelope squirrel housed individually in the laboratory at 25°C. The data were collected and are plotted with 6-minute resolution.

**Table 2.** Parameters of the body temperature rhythm of 93 species of mammals and birds.

Species	Mean °C	Range °C	Phase h	Source
<i>Acomys russatus</i>	36.2	1.5	18	[152]
<i>Acomys russatus</i>	37.1	2.5	18	[125]
<i>Aethomys namaquensis</i>	36.0	2.0	17	[153]
<i>Aethomys namaquensis</i>	36.8	3.9	18	[129]
<i>Alces alces</i>	37.8	0.7	12	[377]
<i>Ammospermophilus leucurus</i>	36.4	4.6	6	[306]
<i>Antechinus stuartii</i>	36.5	3.1	19	[263]
<i>Antidorcas marsupialis</i>	39.4	1.1	12	[371]
<i>Aotus trivirgatus</i>	37.8	1.4	18	[199]
<i>Apodemus flavicollis</i>	37.4	1.7	17	[132]
<i>Apodemus flavicollis</i>	38.0	3.0	15	[166]
<i>Apodemus mystacinus</i>	38.4	2.2	17	[125]
<i>Arvicanthis ansorgei</i>	38.6	3.0	6	[79]
<i>Arvicanthis niloticus</i>	37.5	2.2	6	[134]
<i>Arvicanthis niloticus</i>	37.5	2.1	6	[154]
<i>Arvicanthis niloticus</i>	37.6	1.7	5	[135]
<i>Bettongia gaimardi</i>	37.4	1.7	22	[264]
<i>Bos taurus</i>	38.1	0.4	10	[198]
<i>Bos taurus</i>	38.2	0.9	18	[33]
<i>Bos taurus</i>	38.3	1.4	14	[189]
<i>Bos taurus</i>	38.7	0.8	10	[191]
<i>Bos taurus</i>	39.2	0.9	12	[315]
<i>Bos taurus</i>	39.8	1.0	18	[192]
<i>Callithrix jacchus</i>	37.4	3.0	5	[210]
<i>Callithrix jacchus</i>	37.5	3.0	6	[209]
<i>Callithrix jacchus</i>	37.5	3.0	6	[217]
<i>Callospermophilus lateralis</i>	36.5	4.0	6	[148]
<i>Camelus dromedarius</i>	37.4	1.0	10	[453]
<i>Camelus dromedarius</i>	37.4	2.0	10	[262]
<i>Camelus dromedarius</i>	37.9	0.8	10	[285]
<i>Canis familiaris</i>	38.7	0.7	11	[176]
<i>Canis familiaris</i>	39.0	0.8	11	[174]
<i>Canis familiaris</i>	39.1	0.5	11	[172]
<i>Canis familiaris</i>	39.2	0.4	12	[175]
<i>Capra hircus</i>	38.5	0.7	13	[183]
<i>Capra hircus</i>	38.8	1.0	10	[179]
<i>Capra hircus</i>	38.9	0.7	14	[434]
<i>Capra hircus</i>	39.0	0.4	16	[433]
<i>Capra hircus</i>	39.0	0.8	10	[184]
<i>Capra ibex</i>	39.0	1.0	11	[185]
<i>Cebus albifrons</i>	37.2	2.7	6	[200]
<i>Columba livia</i>	40.0	2.1	6	[415]
<i>Columba livia</i>	40.3	2.7	6	[394]
<i>Columba livia</i>	41.5	1.5	6	[287]
<i>Coturnix coturnix</i>	41.0	1.3	15	[289]
<i>Cryptomys hottentotus</i>	35.2	0.8	18	[454]
<i>Ctenomys knighti</i>	36.6	1.1	18	[163]
<i>Cynomys ludovicianus</i>	37.4	2.5	7	[265]
<i>Dasyurus novemcinctus</i>	35.5	2.6	18	[266]
<i>Dasyurus viverrinus</i>	36.5	3.6	18	[273]
<i>Didelphis marsupialis</i>	35.5	2.5	19	[267]
<i>Didelphis virginiana</i>	35.4	4.0	20	[267]
<i>Dryomys laniger</i>	36.4	5.6	16	[155]
<i>Equus asinus</i>	37.1	2.1	8	[262]
<i>Equus caballus</i>	37.4	1.0	12	[195]
<i>Equus caballus</i>	38.0	0.9	14	[194]
<i>Equus caballus</i>	38.3	1.0	14	[188]
<i>Erinaceus europaeus</i>	35.4	1.2	16	[342]
<i>Eulemur fulvus</i>	38.0	0.9	18	[208]
<i>Felis catus</i>	37.9	1.3	16	[169]
<i>Felis catus</i>	38.0	1.3	19	[173]
<i>Felis catus</i>	38.3	1.0	15	[170]
<i>Felis catus</i>	38.4	0.5	14	[171]
<i>Gallus domesticus</i>	40.2	1.1	12	[298]

(Continued)



**Table 2.** (Continued).

Species	Mean °C	Range °C	Phase h	Source
<i>Gallus domesticus</i>	40.2	1.5	6	[297]
<i>Gallus domesticus</i>	40.7	2.2	8	[291]
<i>Gallus domesticus</i>	40.8	0.8	6	[295]
<i>Geocolaptes olivaceus</i>	40.0	3.8	12	[36]
<i>Glaucomys volans</i>	37.1	2.1	17	[652]
<i>Heterocephalus glaber</i>	33.8	3.8	15	[268]
<i>Homo sapiens</i>	36.5	1.2	10	[219]
<i>Homo sapiens</i>	36.7	1.1	10	[227]
<i>Homo sapiens</i>	36.8	0.8	8	[235]
<i>Homo sapiens</i>	36.8	0.8	10	[231]
<i>Homo sapiens</i>	36.8	0.7	10	[520]
<i>Homo sapiens</i>	36.8	1.2	10	[233]
<i>Homo sapiens</i>	36.9	1.2	10	[247]
<i>Homo sapiens</i>	36.9	1.0	8	[224]
<i>Homo sapiens</i>	36.9	1.0	7	[26]
<i>Homo sapiens</i>	36.9	0.9	11	[323]
<i>Homo sapiens</i>	37.0	1.0	10	[654]
<i>Homo sapiens</i>	37.0	1.0	8	[250]
<i>Homo sapiens</i>	37.0	1.2	9	[324]
<i>Homo sapiens</i>	37.0	1.1	10	[226]
<i>Homo sapiens</i>	37.0	1.3	10	[228]
<i>Homo sapiens</i>	37.0	1.2	10	[230]
<i>Homo sapiens</i>	37.0	0.8	10	[240]
<i>Homo sapiens</i>	37.0	1.0	9	[242]
<i>Homo sapiens</i>	37.0	0.8	10	[255]
<i>Homo sapiens</i>	37.1	1.0	11	[241]
<i>Homo sapiens</i>	37.6	1.6	10	[234]
<i>Ictidomys tridecemlineatus</i>	36.4	5.0	7	[380]
<i>Ictidomys tridecemlineatus</i>	36.7	4.2	8	[39]
<i>Isoodon macrourus</i>	36.2	2.5	16	[267]
<i>Isoodon obesulus</i>	36.5	2.5	13	[282]
<i>Lama glama</i>	38.5	1.4	6	[376]
<i>Lama glama</i>	38.5	1.2	10	[375]
<i>Lasiorhinus latifrons</i>	35.3	2.9	16	[269]
<i>Loxodonta africana</i>	36.5	1.3	12	[286]
<i>Macaca fuscata</i>	37.0	2.4	9	[201]
<i>Macaca mulatta</i>	36.8	1.4	10	[203]
<i>Macaca mulatta</i>	37.0	1.8	9	[211]
<i>Macaca mulatta</i>	37.2	1.0	9	[325]
<i>Macaca mulatta</i>	38.1	1.6	10	[202]
<i>Macaca nemestrina</i>	38.0	2.0	8	[212]
<i>Macropus giganteus</i>	34.6	2.8	19	[270]
<i>Macropus rufus</i>	36.3	1.7	17	[270]
<i>Marmota monax</i>	37.7	1.3	10	[137]
<i>Meleagris gallopavo</i>	40.2	1.2	12	[299]
<i>Mephitis mephitis</i>	36.4	1.3	12	[117]
<i>Meriones libycus</i>	37.3	1.4	18	[374]
<i>Meriones unguiculatus</i>	36.9	2.7	8	[157]
<i>Meriones unguiculatus</i>	37.4	2.7	14	[39]
<i>Mesocricetus auratus</i>	36.0	2.9	14	[39]
<i>Mesocricetus auratus</i>	36.8	1.7	18	[121]
<i>Mesocricetus auratus</i>	36.9	2.5	17	[648]
<i>Mesocricetus auratus</i>	38.0	1.3	17	[119]
<i>Microcebus murinus</i>	36.3	2.8	18	[431]
<i>Microcebus murinus</i>	36.5	2.5	18	[387]
<i>Microcebus murinus</i>	36.6	2.5	18	[204]
<i>Microcebus murinus</i>	36.8	2.0	16	[432]
<i>Microcebus murinus</i>	36.8	2.3	17	[213]
<i>Monodelphis domestica</i>	34.3	6.5	15	[283]
<i>Mus musculus</i>	36.0	2.0	15	[109]
<i>Mus musculus</i>	36.1	2.0	18	[107]
<i>Mus musculus</i>	36.2	2.4	17	[326]
<i>Mus musculus</i>	36.3	2.2	16	[94]
<i>Mus musculus</i>	36.5	1.8	21	[113]

(Continued)

Table 2. (Continued).

Species	Mean °C	Range °C	Phase h	Source
<i>Mus musculus</i>	36.6	2.2	18	[97]
<i>Mus musculus</i>	36.6	2.1	19	[88]
<i>Mus musculus</i>	36.6	2.0	16	[108]
<i>Mus musculus</i>	36.7	1.6	19	[89]
<i>Mus musculus</i>	36.8	1.7	18	[93]
<i>Mus musculus</i>	36.8	2.1	18	[104]
<i>Mus musculus</i>	36.8	2.2	20	[105]
<i>Mus musculus</i>	36.9	2.2	16	[92]
<i>Mus musculus</i>	37.0	2.0	17	[40]
<i>Myrmecobius fasciatus</i>	35.0	5.8	10	[412]
<i>Nasua nasua</i>	37.5	1.9	7	[271]
<i>Octodon degus</i>	36.4	1.6	8	[450]
<i>Octodon degus</i>	36.5	2.0	5	[142]
<i>Octodon degus</i>	36.8	2.5	11	[39]
<i>Octodon degus</i>	37.0	1.7	5	[139]
<i>Octodon degus</i>	37.2	1.8	8	[651]
<i>Octodon degus</i>	37.3	2.0	6	[140]
<i>Odocoileus hemionus</i>	38.3	1.8	12	[279]
<i>Oryctolagus cuniculus</i>	38.9	0.9	20	[272]
<i>Oryctolagus cuniculus</i>	39.8	0.8	12	[117]
<i>Oryx leucoryx</i>	37.8	3.0	7	[373]
<i>Otospermophilus beecheyi</i>	36.4	2.4	5	[147]
<i>Ovis aries</i>	38.2	1.0	9	[186]
<i>Ovis aries</i>	38.5	0.3	5	[372]
<i>Ovis aries</i>	38.7	1.0	9	[180]
<i>Ovis aries</i>	39.3	0.3	14	[433]
<i>Ovis aries</i>	39.6	2.0	13	[187]
<i>Ovis aries</i>	40.4	1.3	9	[178]
<i>Pachyuromys duprasi</i>	36.5	2.5	18	[28]
<i>Papio hamadryas</i>	37.9	1.7	8	[214]
<i>Petaurus breviceps</i>	37	3.2	18	[284]
<i>Procyon lotor</i>	38.1	1.4	1	[117]
<i>Rattus norvegicus</i>	36.8	2.5	16	[57]
<i>Rattus norvegicus</i>	36.9	1.8	18	[60]
<i>Rattus norvegicus</i>	37	2.1	18	[327]
<i>Rattus norvegicus</i>	37	1.9	19	[51]
<i>Rattus norvegicus</i>	37	1.8	18	[65]
<i>Rattus norvegicus</i>	37	1.7	18	[52]
<i>Rattus norvegicus</i>	37.1	1.8	18	[73]
<i>Rattus norvegicus</i>	37.2	1.5	17	[45]
<i>Rattus norvegicus</i>	37.2	1.5	17	[50]
<i>Rattus norvegicus</i>	37.2	1.0	18	[86]
<i>Rattus norvegicus</i>	37.3	2.1	16	[39]
<i>Rattus norvegicus</i>	37.3	1.0	18	[645]
<i>Rattus norvegicus</i>	37.3	1.4	18	[328]
<i>Rattus norvegicus</i>	37.4	1.4	18	[43]
<i>Rattus norvegicus</i>	37.4	1.3	18	[396]
<i>Rattus norvegicus</i>	37.4	1.2	−1	[612]
<i>Rattus norvegicus</i>	37.4	1.4	18	[308]
<i>Rattus norvegicus</i>	37.4	1.6	18	[429]
<i>Rattus norvegicus</i>	37.5	1.5	18	[77]
<i>Rattus norvegicus</i>	37.5	2.0	18	[44]
<i>Rattus norvegicus</i>	37.5	1.4	18	[428]
<i>Rattus norvegicus</i>	37.5	1.3	18	[40]
<i>Rattus norvegicus</i>	37.5	1.4	18	[88]
<i>Rattus norvegicus</i>	37.5	1.2	18	[80]
<i>Rattus norvegicus</i>	37.6	1.1	18	[41]
<i>Rattus norvegicus</i>	37.6	1.2	16	[47]
<i>Rattus norvegicus</i>	37.6	1.7	19	[329]
<i>Rattus norvegicus</i>	37.7	1.3	17	[46]
<i>Rattus norvegicus</i>	37.8	1.8	18	[79]
<i>Rhabdomys pumilio</i>	36.6	2.0	5	[153]
<i>Saimiri sciureus</i>	37.5	2.0	8	[378]
<i>Saimiri sciureus</i>	37.5	2.7	6	[610]

(Continued)

**Table 2.** (Continued).

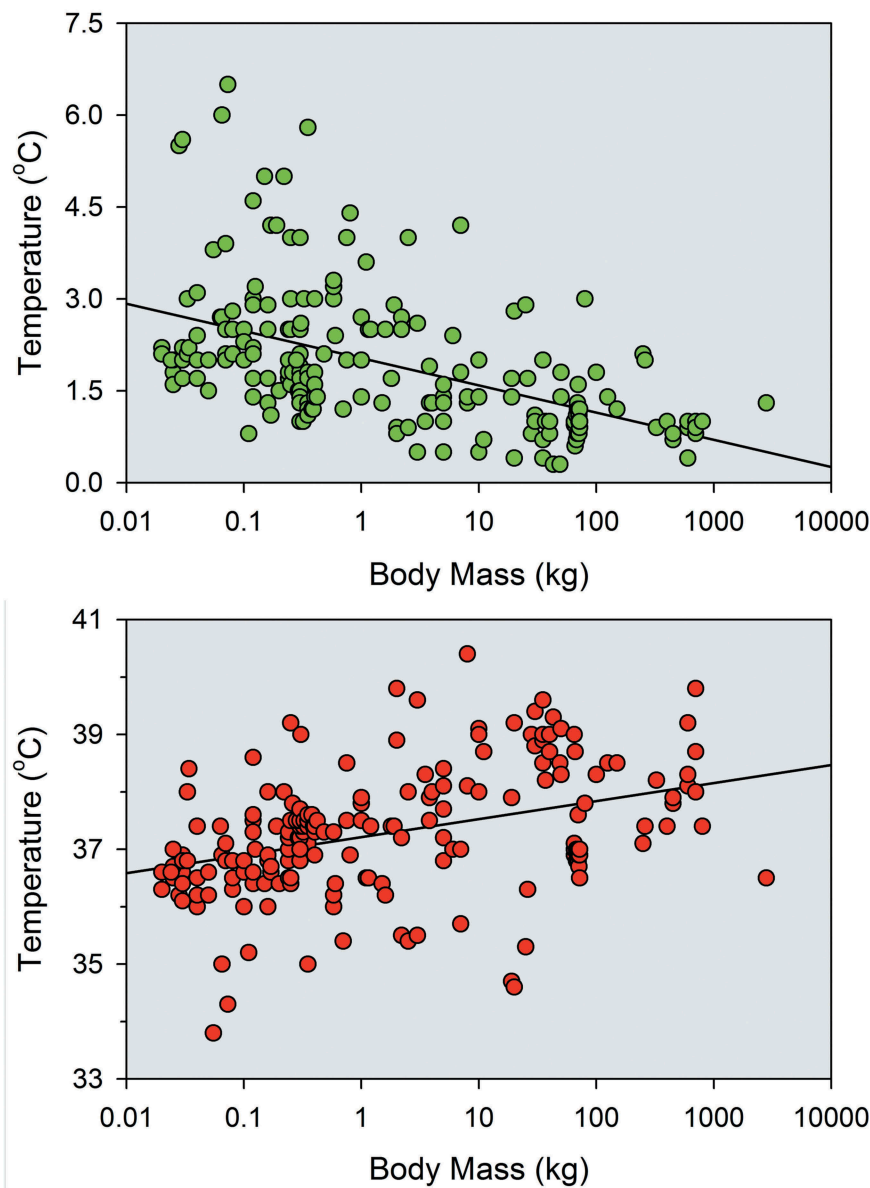
Species	Mean °C	Range °C	Phase h	Source
<i>Saimiri sciureus</i>	37.9	2.0	7	[313]
<i>Sarcophilus harrisii</i>	35.7	4.2	18	[273]
<i>Sciurus carolinensis</i>	37.3	3.0	5	[156]
<i>Sciurus vulgaris</i>	39.0	2.6	6	[161]
<i>Sminthopsis macroura</i>	36.2	5.5	18	[409]
<i>Spalax ehrenbergi</i>	36.4	1.5	5	[446]
<i>Spermophilus xanthoprimum</i>	37.0	4.0	7	[35]
<i>Struthio camelus</i>	39.1	1.8	9	[300]
<i>Sturnus vulgaris</i>	40.1	3.2	7	[303]
<i>Suncus murinus</i>	35.0	6.0	14	[29]
<i>Sus scrofa</i>	38.7	0.6	12	[280]
<i>Sus scrofa</i>	39.0	1.4	14	[275]
<i>Sus scrofa</i>	39.6	0.5	9	[274]
<i>Tamiasciurus hudsonicus</i>	39.2	2.5	6	[131]
<i>Thallomys nigricauda</i>	36.8	2.1	18	[150]
<i>Thallomys paedulus</i>	36.6	2.9	18	[129]
<i>Trichosurus vulpecula</i>	37.4	2.9	16	[267]
<i>Tupaia belangeri</i>	37.4	4.2	6	[652]
<i>Tupaia belangeri</i>	38.0	5.0	5	[27]
<i>Tyto alba</i>	40.3	2.2	17	[414]
<i>Urocitellus parryi</i>	36.9	4.4	8	[346]
<i>Urocitellus parryi</i>	37.5	2.0	7	[348]
<i>Urocitellus parryi</i>	38.5	4.0	6	[158]
<i>Urocitellus richardsonii</i>	36.0	3.2	6	[164]
<i>Urocitellus richardsonii</i>	36.2	3.3	10	[39]
<i>Vombatus ursinus</i>	34.7	1.4	18	[278]

from study to study within the same species, possibly because of methodological differences, but intraspecies differences are most often smaller than interspecies differences. Although not inferable from the data shown in the table, it should also be pointed out that intraindividual differences within a species are usually smaller than interindividual differences [322].

In terms of the mean level of body temperature, a noticeable trend in Table 2 is that the body temperature of birds tends to be more than 3 °C higher than that of mammals (on average, 41°C and 37.5 °C, respectively), and the temperature of marsupial mammals tends to be about 3°C lower than that of placental mammals. The range of oscillation also varies greatly from species to species, being noticeably wider in squirrels than in other rodents of comparable body size. The acrophase (peak time) is generally consistent with the temporal niche of the species, in the sense that the acrophase usually occurs at night (i.e., more than 12 hours after lights-on) for nocturnal animals and during the day for diurnal animals, although farm animals tend to have unusually late acrophases (sometimes extending into the early dark phase).

A few broad interspecies comparisons of parameters of the body temperature rhythm have been previously made by other scholars. Aschoff noticed that the amplitude of the temperature rhythm is 3 to 6 times smaller in large animals than in small animals in the body mass range from 10 g to 1 kg [330]. Based on data from 206 independent studies in various laboratories, I can confirm that the amplitude is about 3 times narrower in larger mammals for the full range of body weight from 10 g to 2,000 kg, as shown in Figure 3 (upper panel). Presumably, large bodies can buffer the effects of the oscillations in heat production and heat loss that are responsible for the body temperature rhythm. Interestingly, body size also has an effect on the mean level of the temperature rhythm (Figure 3, lower panel). Animals in the 1,000 kg range have, on average, body temperatures 1.4 °C higher than the body temperatures of animals in the 10 g range. Again, this is presumably due to the greater thermal inertia of large animals. It should be pointed out that, in both cases (amplitude and mean temperature), the correlation with body mass is statistically significant but is far from perfect ( $r = -0.51$  and  $r = 0.38$ , respectively). This may explain why Lovegrove failed to find a correlation between body size and mean body temperature in a set of 267 studies in



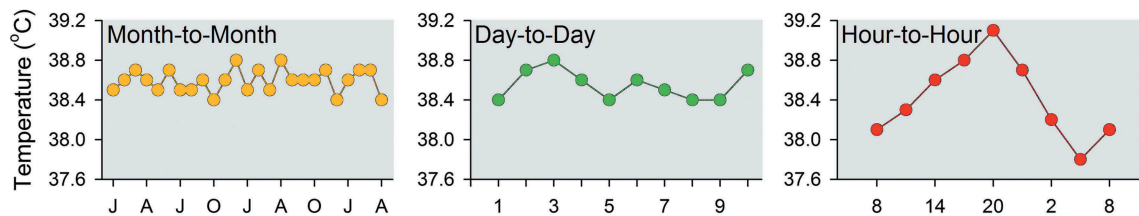


**Figure 3.** Parameters of the body temperature rhythm as a function of body mass as determined for 86 mammalian species in 206 published studies. Top: daily range of oscillation of the body temperature rhythm. Bottom: mean level of the body temperature rhythm.

animals weighing under 1 kg [331]. Given the very wide spread of data seen in Figure 3, it is to be expected that large differences in body size would be needed for the detection of a significant correlation. Mortola and Lanthier surveyed 125 studies in mammals ranging from 10 g to 5,000 kg and did find that the amplitude of the body temperature rhythm is smaller, and the mean level is higher, in large animals than in small animals [332]. Hetem and colleagues found a large reduction (rather than increase) in mean body temperature with increase in body mass above 10 kg in 17 species of large mammalian herbivores [333], but the evaluated studies were conducted in the

wild, where food and water shortages were likely to affect body temperature, as discussed below.

Most studies of the body temperature rhythm are conducted over a few days and cannot provide evidence regarding the long-term stability of the rhythm. A study conducted on four species of farm animals over two years provided valuable information about the variability of the parameters of the body temperature rhythm over days and months [334]. As shown for a single bovine in Figure 4, the normal circadian range of oscillation is wider than the range of oscillation of same-time-of-day values over days or months. This animal had full unrestricted access to food and



**Figure 4.** Rectal temperature of a female bovine (*Bos taurus*) as measured on three time scales: month-to-month (evening measurements conducted monthly for two years), day-to-day (evening measurements conducted daily for 10 days), and hour-to-hour (measurements conducted every 3 hours over a single day). The abscissas of the three plots are marked in months, days, and hours, respectively.

water, but ambient temperature ranged from 8°C in the winter to 30°C in the summer, and the stability of same-time-of-day values over months emphasizes the excellence of homeothermic control of body temperature in farm animals. Of course, not all species have such good control of their core temperature, and many small rodents put homeothermy on hold during the winter and engage in hibernation [22,23,335,336]. A few studies have suggested that circadian rhythmicity of body temperature is preserved during hibernation (albeit with very small amplitude) [337–340], but many other studies have found no body temperature rhythm in hibernating animals [35,341–348].

A truly endogenous rhythm must persist (with a slightly different period) in the absence not only of environmental cycles of ambient temperature and food availability but also in the absence of a light-dark cycle. Much fewer studies have been conducted under conditions of constant darkness (or constant light), but the endogenous nature of the body temperature rhythm has been confirmed in many species of birds and animals, as shown in Table 3. Of course, the fact that the body temperature rhythm free-runs under constant environmental conditions is proof only of the existence of an endogenous circadian clock. It is not proof that the body generates a temperature rhythm as a fundamental process. The rhythmicity of body temperature could be simply a side effect of the rhythmicity of another endogenously generated process. This matter will be discussed further below.

### Exogenous determinants

Studies of the body temperature rhythm conducted in the outdoors have demonstrated that variations in day length, ambient temperature, food and water availability, predator danger, and other variables can affect the body temperature rhythm of free-ranging animals [38,370–377]. Unfortunately, studies conducted in the wild are almost always correlational and cannot differentiate the action of the various environmental factors, but studies conducted under controlled laboratory conditions have confirmed the specific effects of ambient temperature and food availability.

Regarding ambient temperature, several studies have described an increase in the amplitude of the body temperature rhythm in animals exposed chronically to ambient temperatures below thermoneutrality. This phenomenon has been described in squirrel monkeys [378], tree shrews [379], thirteen-lined ground squirrels [380], sheep [381], pigeons [382], mousebirds [383], and sunbirds [384]. On the other hand, no effect of ambient temperature on the amplitude of the body temperature rhythm was found in rats [385,386], mouse lemurs [387], or golden hamsters and fat-tailed gerbils [379]. Genuine species differences may be responsible for the conflicting results.

Regarding food availability, it has long been known that fasted animals experience a reduction in metabolic rate and a fall in body temperature [388–399]. What is especially interesting about

**Table 3.** Studies documenting the existence of circadian (free-running) rhythmicity of body temperature.

Rodents	[41, 52, 60, 65–67, 72, 76, 79, 80, 90, 103, 104, 106, 118, 122, 134, 141, 142, 152, 162, 163, 306, 328, 346, 348–356, 380, 446, 450, 454, 612, 629]
Non-human primates	[199, 202, 204, 206–208, 213, 216, 313, 325, 431, 469]
Humans	[218, 230, 232, 233, 242, 357–366]
Other mammals	[27, 169–171, 178, 188, 266, 275, 285, 338, 367, 368, 453]
Birds	[287–291, 293, 295–297, 299, 303, 369, 382, 413]

this phenomenon is its modulation by the circadian system. The hypothermia induced by food deprivation (or chronic food restriction) does not occur indiscriminately; rather, it is restricted to the inactive phase of the circadian cycle. Some animals have a natural disposition to exhibit daily torpor even when fed regularly [380,400–412], but various true homeotherms exhibit circadian-modulated starvation-induced hypothermia. This has been documented in doves [413], owls [414], pigeons [394,395,415–417], quail [418], mousebirds [383,419], finches [420], pygmy mice [421], deer mice [422], domestic mice [423–425], rats [396,397,426–430], lemurs [431,432], sheep [433], goats [434], and camels [435].

To avoid misunderstandings, it should be stressed that any event in the environment, whether rhythmic or not, can disturb (“mask”) circadian rhythms. True synchronization (“entrainment”) of circadian rhythms has long been known to be produced by the light-dark cycle [436–438], but it can also be produced by cycles of ambient temperature [439–455] and food availability [456–481]. A study in mice provided the suggestion that cycles of ambient temperature may be as effective as light-dark cycles in producing entrainment but may not be as effective in the production of masking [452], and further studies are needed to confirm this observation. The control of circadian rhythms in the wild is likely determined just as much by the influence of entrainment as by the influence of masking on the endogenously-generated rhythms [482,483].

## Circadian rhythmicity of metabolism

### Research methodology

For the monitoring of whole-organism metabolism, three techniques are well established: direct calorimetry, indirect calorimetry, and the isotopic tracer technique [484]. The isotopic tracer technique is convenient for field studies, but it does not provide the temporal resolution needed for the study of circadian rhythms. In laboratory studies, direct calorimetry is the “gold standard” for accurate measurement of whole-organism metabolism, but indirect calorimetry is by far the most commonly used technique [485].

Indirect calorimetry is based on the measurement of oxygen consumed (and carbon dioxide

produced) by the organism and on the chemical properties of oxidation. Knowledge of the stoichiometric properties of oxidative processes makes it possible to calculate the amount of nutrient being combusted, and the amount of heat being released, by measuring only the amount of oxygen being consumed. To measure the concentration of oxygen in the air used by the organism (as well as the concentration of carbon dioxide, if greater accuracy is needed in the computation of metabolic rate), gas analyzers are employed. Suppliers of gas analyzers for biomedical research include Servomex (Crowborough, England), Columbus Instruments (Columbus, Ohio), Sable Systems International (North Las Vegas, Nevada), and Qubit Systems (Kingston, Canada). For data collection the animal of interest is placed inside a sealed chamber, and a measured volume of air is passed through the chamber. By determining the difference in the concentration of oxygen in the air that enters the chamber and in the air that leaves the chamber, one can determine the percentage of oxygen consumed by the organism. The percentage can then be converted into amount of oxygen (and corresponding amount of heat produced) if the exact flow of air through the chamber is known [486,487]. A computerized system that activates the air-switch valves and collects the data is needed for the monitoring of metabolism with adequate temporal resolution for long-term studies of circadian rhythmicity.

### Endogenous determinants

Daily and/or circadian rhythmicity in whole-organism metabolism has been documented in mammals and birds, as shown in Table 4. Most studies have been conducted on rodents, but other animals have been studied as well.

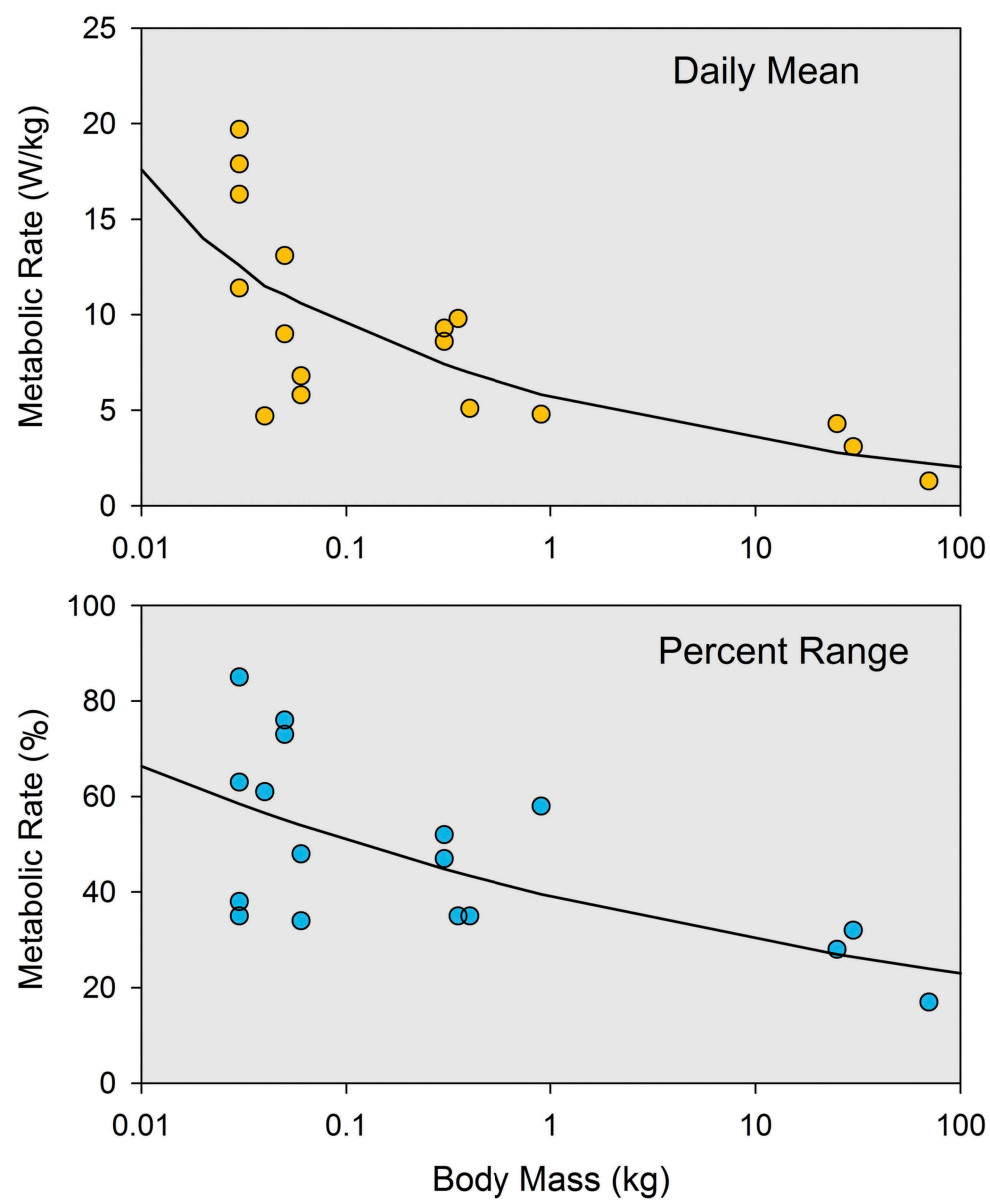
It has long been known that, when expressed per unit of body mass, metabolic rate is higher in small animals than in large animals [516–519]. It is not surprising, therefore, to find out that the mean level of the daily rhythm of metabolism is higher in small animals than in large animals, as shown in Figure 5 (upper panel). This figure was prepared with data from 17 of the 61 studies listed in Table 4. Only studies that involved mammals and provided sufficient information for conversion of the results to the

**Table 4.** Studies documenting the existence of daily rhythmicity of whole-organism metabolism.

Rats	[42, 43, 62, 63, 81, 83, 86, 428, 488–496, 611, 612]
Other rodents	[28, 103, 125, 128, 143, 146, 150, 312, 400, 424, 497–504, 521, 628]
Humans	[248, 505, 506, 520, 602]
Other mammals	[266, 268, 270, 271, 277, 313, 507–511]
Birds	[298, 394, 405, 414, 512–515]

common unit of W/kg were used. Of special interest are the data on percent range shown in the lower panel of the figure. Percent range is the range of daily

oscillation expressed as a percentage of the daily mean, and it is used instead of the absolute value because the interspecies differences in mean values are quite large, so that the range for each species is meaningful only in reference to the mean for that species. Thus, for example, humans (70 kg) had a mean metabolic rate of 1.3 W/kg with a range of oscillation of 0.2 W/kg, so that the percent range was 15% [520]. In contrast, domestic mice (30 g) had a mean metabolic rate of 17.9 W/kg with a range of oscillation of 15.2 W/kg, so that the percent range was 85% [521], which is much greater than the



**Figure 5.** Mean level (upper plot) and range of oscillation (lower plot) of the daily rhythm of metabolism as a function of body mass in various mammalian species. The range of oscillation is expressed as a percentage of the daily mean ("Percent range"). The data were obtained from 17 published studies and converted to the common unit of W/kg.

percent range in humans. As was the case for the body temperature rhythm, different studies on the same species were somewhat variable but relatively consistent. For example, a different study on domestic mice reported a mean metabolic rate of 19.7 W/kg with a range of oscillation of 12.4 W/kg, so that the percent range was 63% [424], thus smaller than in the other mouse study but still larger than in humans.

Although not in the scope of this article, it should be mentioned that the circadian modulation of metabolism has been studied at the cellular level, and several reviews of the literature have been written [522–524].

### **Exogenous determinants**

While scant attention has been given to environmental factors that specifically affect the circadian rhythm of metabolism, there exists an extensive literature on the general effect of environmental factors on steady-state metabolism. As was the case concerning body temperature, the effects of changes in ambient temperature and food availability have been particularly well studied.

Birds and mammals can increase metabolic heat production when exposed to a cold environment, and this is called cold-induced thermogenesis. Shivering is one form of cold-induced thermogenesis. It is a widespread mechanism of thermogenesis used to prevent the fall of body temperature in a cold environment. It consists of small-amplitude, high-frequency contractions of skeletal muscles. It is employed both by birds [382,392,525–531] and by mammals [532–547], including humans [548–550]. Forms of biological thermogenesis other than shivering are collectively called non-shivering thermogenesis. Birds seem to rely primarily on shivering and, if they exhibit thermoregulatory non-shivering thermogenesis, the muscles themselves are the probable source [392,528–530,551–554]. Mammals, on the other hand, use non-shivering thermogenesis extensively in response to cold stress, and the capacity to use it is strongly affected by acclimation or acclimatization [534,540–543,546,555–578]. Mammalian thermoregulatory non-shivering thermogenesis often relies on the

activation of a specialized tissue, brown adipose tissue [579,580].

The effects of food availability, and food intake more specifically, are usually discussed as part of the phenomenon of diet-induced thermogenesis. Diet-induced thermogenesis is the fraction of energy expenditure induced by the ingestion of food, and some authors include basal metabolic rate in the definition of diet-induced thermogenesis [581]. There are two types of diet-induced thermogenesis. The first type is called obligatory because it cannot be avoided. After a meal is ingested, metabolic rate is temporarily elevated [520,582–591], and this elevation is believed to be due partially to the energetic cost of digestion and partially to a cephalic component involving mastication as well as arousal [592–598]. The other type of diet-induced thermogenesis is called adaptive because its magnitude can be adapted to conditions of shortage or excess of food supply. That is, diet-induced thermogenesis can be increased after overeating and be reduced during starvation or food restriction [583,599–608]. As was the case for cold-induced thermogenesis, diet-induced thermogenesis in mammals seems to depend strongly on the activation of brown adipose tissue [609].

## **Relationship of body temperature and metabolism at the organismal level**

### **Autonomy of the body temperature rhythm**

The previous sections described the rhythms of body temperature and metabolism separately, but it is well known that body temperature and metabolism can affect each other in both directions. Changes in body temperature can cause changes in metabolism by affecting the rate of chemical reactions in the body (and by inducing a thermogenic response), and changes in metabolism are accompanied by changes in metabolic heat production, which, in the absence of compensatory changes in heat loss, will cause a change in body temperature. Studies in which body temperature and metabolic rate have been recorded simultaneously have shown that the two variables oscillate together through the day [313,520,610–612], and the obvious question to ask is whether there is a causal link – and, if so, in which direction.



The question must be asked because changes in body temperature are the result of the balance between heat production and heat loss, and a rise in heat production will not elevate temperature if it is compensated by an equal rise in heat loss.

Studies conducted on reptiles have shown that endogenously-controlled rhythmicity of body temperature is present in extant ectotherms, the control being achieved by behavioral selection of suitable thermal environments [613–616]. For this reason, it is sensible to assume that the evolution of circadian rhythmicity of body temperature preceded the evolution of endothermy in mammals and birds. In fact, it is believed that endothermy evolved about 70 million years ago [617–619], much after the evolution of circadian rhythmicity 2.5 billion years ago [620]. Thus, one can suggest that the ability to adjust metabolic rate evolved to either directly or indirectly facilitate the circadian oscillation of body temperature, even if basal metabolic rate and body temperature seem to have evolved separately from each other [621]. In other words, the rhythm of body temperature must not be a side effect of the rhythm of metabolic thermogenesis; rather, the rhythm of body temperature must require the rhythmic modulation of metabolic thermogenesis. That the rhythm of body temperature is not a simple side effect of the rhythm of metabolic thermogenesis associated with changes in locomotor activity has been demonstrated experimentally both in humans and in other animals, as described in the next two paragraphs.

In order to investigate the potential causal link between the locomotor activity rhythm (which is a major thermogenic process) and the temperature rhythm, several researchers recorded the body temperature rhythm of human subjects maintained in continuous bed rest [622–624] or undergoing a constant routine protocol, which involves bed rest as well as sleep deprivation and the ingestion of frequent, equal-size meals [520,625–627]. Although the amplitude of the rhythm was reduced under this condition of constant physical inactivity, robust rhythmicity of body temperature persisted. Thus, while the activity rhythm may alter the amplitude and shape of the body temperature rhythm, it does not cause it.

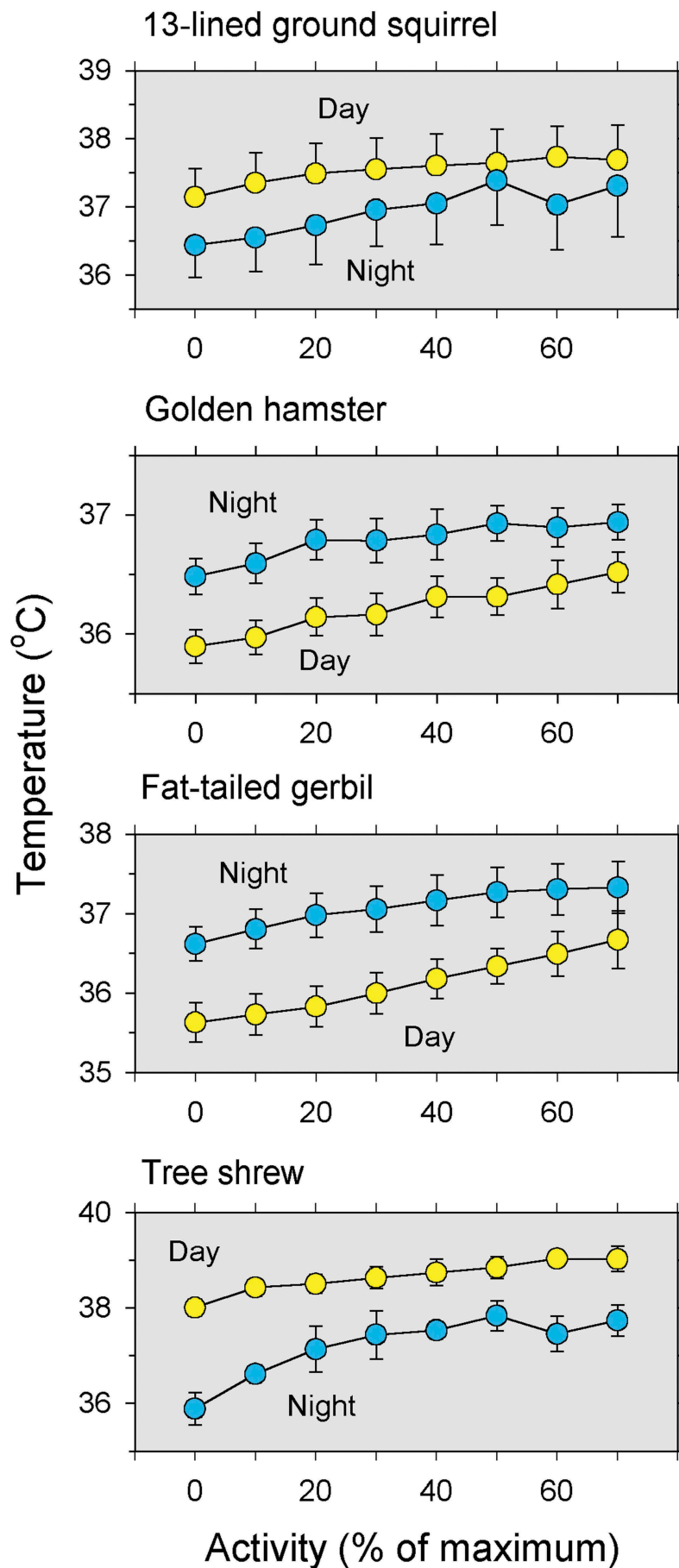
Bed rest cannot be used with animals – because they do not comply with requests for voluntary rest – but one can look at the day-night difference in the correlation between the rhythms of activity and

temperature. It has been found that, although nocturnal animals are generally more active at night than during the day, their body temperature is higher at night regardless of the actual activity level [628–632]. Conversely, the body temperature of diurnal animals is higher during the day regardless of the actual activity level [306,633]. These relationships are illustrated in Figure 6 for four different species of small mammals. Notice that, for the nocturnal animals (golden hamster and fat-tailed gerbil), body temperature is higher at night for all levels of activity, even though there is a small effect of activity level on body temperature. For the diurnal animals (13-lined ground squirrel and tree shrew), body temperature is higher during the day for all levels of activity [633]. Thus, it can be inferred that the body temperature rhythm in animals, as in humans, is not caused by the activity rhythm. That is, the body temperature rhythm is not a side effect of the metabolism rhythm associated with changes in activity. This conclusion brings us back to the question of whether the body generates (or attempts to generate) a temperature rhythm as a fundamental process of life.

In ectotherms, a rhythm of body temperature can only be produced by behavioral selection of cooler or warmer environments, but, in endotherms, endogenous heat production (through shivering or non-shivering thermogenesis) is possible. Because endogenous heat production is also at the service of homeothermy, it is not immediately evident whether the circadian system or the thermoregulatory system is in control of thermogenesis at any given time. This uncertainty is reflected in a controversy about a hypothetical circadian modulation of the thermoregulatory set point.

Half a century ago, most thermal physiologists endorsed the engineering model of homeostatic body temperature regulation by an adjustable set point [634,635]. In the 1980's, however, a number of thermal physiologists abandoned the set point theory and adopted the viewpoint that there is no master reference-signal generator and that individual effector organs are activated directly by their sensory input [636–639]. Nonetheless, many life scientists assumed that the circadian oscillation in body temperature is primarily under homeostatic control and is secondarily modulated by the circadian system through an oscillation in the thermoregulatory set point [17,313,640,641]. According to

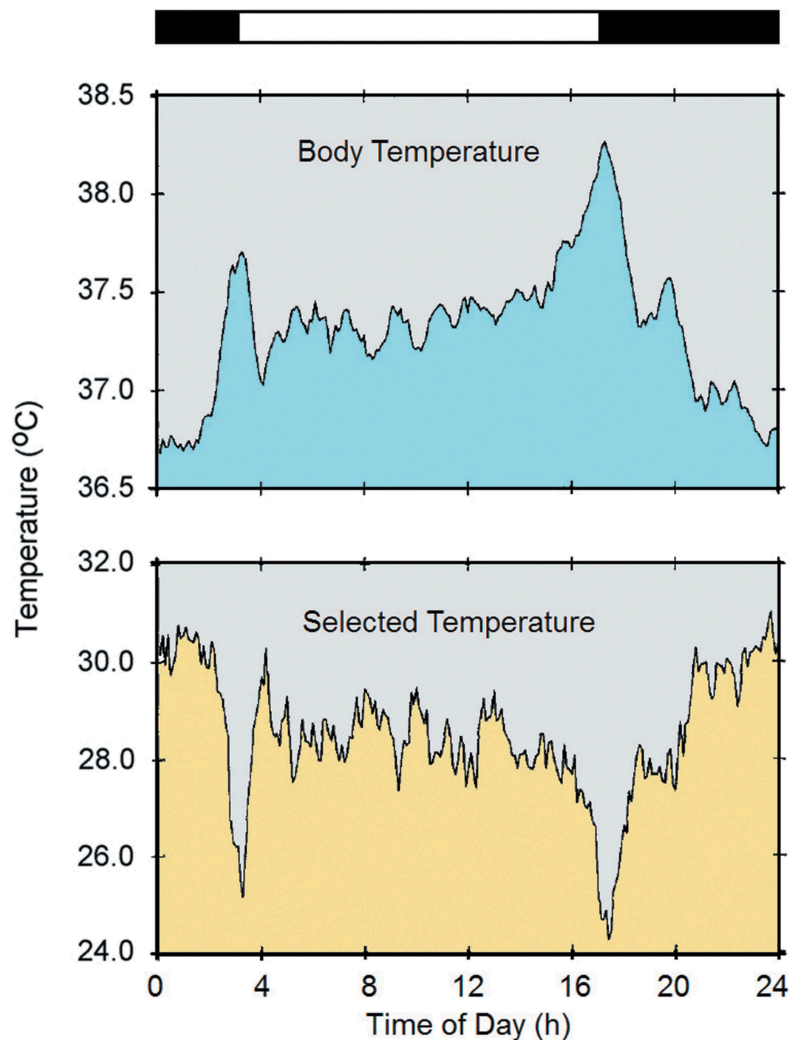




**Figure 6.** Mean body temperatures associated with different levels of locomotor activity during the dark phase (blue) and the light phase (yellow) of the light-dark cycle for four species. Error bars indicate SEM.

this view, the circadian rise in temperature would be a response to an elevation in the thermoregulatory set point, whereas the circadian fall in temperature would be a response to a lowering of the set point. Because circadian rhythmicity is evolutionarily older than homeothermy, however, the assumption of a set point change is contentious. To judge whether there is circadian modulation of the thermoregulatory set point, one must actually measure the set point. One way to do this is to measure the motivation of an organism to counteract an imposed deviation of its internal temperature. Research in many laboratories over the years has documented that higher ambient temperatures are preferred during the phase of low body temperature, and lower ambient

temperatures are preferred during the phase of high body temperature, in rats [30,397,642–646], mice [647], golden hamsters [644,648,649], Siberian hamsters [650], fat-tailed gerbils [28], degus [651], stripe-faced dunnarts [409], tree shrews [652], flying squirrels [652], mouse lemurs [653], and humans [654–658]. An example is given in Figure 7. A degu was housed in a temperature-gradient chamber with ambient temperatures ranging from 14°C to 33°C, and its body temperature and preferred ambient temperature were recorded at 6-minute intervals for 10 or more days [651]. Notice that, as expected for a diurnal animal, body temperature is high during the day and low during the night (upper panel). Also, in accordance with the animal's crepuscular behavior, body



**Figure 7.** Daily rhythms of body temperature and selected ambient temperature of a degu (*Octodon degus*) housed in a temperature-gradient chamber. The white and black bars at the top indicate the light and dark phases of the prevailing light-dark cycle (14L:10D).

temperature shows clear peaks at lights-on and lights-off. Importantly, the rhythm of behavioral temperature selection (lower panel) is 180° out of phase with the rhythm of body temperature, with higher ambient temperatures being selected during the night and lower temperatures during the day. The opposite movement of the two variables is particularly evident at the times of lights-on and lights-off. Clearly, higher environmental temperatures are selected when body temperature is low, and vice versa, indicating that the animal is attempting to counteract the circadian rhythm of body temperature. Thus, the oscillation of the set point cannot possibly be responsible for the temperature rhythm. As a matter of fact, there is no reason to assume that the set point oscillates at all. As body temperature oscillates, the animals behaviorally counteract the oscillation to defend the unaltered set point. The thermoregulatory system actually opposes the oscillation of body temperature imposed by the circadian system [659,660].

The existence of the body temperature rhythm is in itself proof that the thermoregulatory system's opposition to the circadian oscillation of body temperature is not entirely successful. However, the amplitude of the temperature rhythm is effectively reduced by the action of the thermoregulatory system. There are at least two types of supportive evidence for this. One type comes from the comparison of the amplitude of the rhythm in animals maintained in a constant-temperature environment with the amplitude in animals allowed to continually select their environmental temperature in a gradient. The amplitude of the body temperature rhythm was reduced in tree shrews and flying squirrels allowed to select their environmental temperature [652]. The other type of supportive evidence comes from studies in which the thermoregulatory system was impaired by surgical ablation of the main thermoregulatory center in the preoptic area of the brain. The amplitude of the body temperature rhythm was greatly enhanced in rats and golden hamsters with preoptic lesions [661–663]. Thus, ablation of the preoptic area releases the circadian oscillation of body temperature from inhibitory control. This means that the thermoregulatory center in the preoptic area of unlesioned animals restricts the oscillation of body temperature to an acceptable range. That is, in normal

animals, the circadian system generates an oscillatory signal that is communicated to the organs responsible for heat production and heat loss, and at the same time the thermoregulatory system generates a set point that, like most control systems, has a margin of hysteresis error; the integrated output is an oscillation whose amplitude is restricted to the boundaries of hysteresis error. For physiologists who dislike the set point model, the previous sentence can be reworded as follows: in normal animals, the circadian system generates an oscillatory signal that is communicated to the organs responsible for heat production and heat loss, and at the same time independent thermoeffectors are activated to counteract the incipient alteration in body temperature; the integrated output is an oscillation whose amplitude is restricted to the range of activation of the thermoeffectors.

### ***Why there is a body temperature rhythm***

One may wonder why should there be a circadian rhythm of body temperature at all, especially if it is opposed by the thermoregulatory system. The answer is that circadian rhythmicity of body temperature must be evolutionarily adaptive. Circadian rhythmicity is an evolutionarily old trait that most likely existed before the appearance of the first animals [620]. Seeking warm temperatures in anticipation of the active phase of the circadian cycle would have provided an advantage to the original (and extant) ectothermic animals whose ability to perform bodily functions was extremely dependent on ambient temperature [10]. Because homeothermy is found today only in mammals and birds (with a few exceptions), it must have appeared when circadian rhythmicity was already a property of every multicellular organism. As a matter of fact, endothermic homeothermy likely evolved gradually from an ancestral form of heterothermy [619,664]. Thus, in homeotherms, the more recent goal of maintaining homeostasis conflicts with the older goal of causing body temperature to oscillate, and this conflict explains the opposition between the thermoregulatory system and the circadian system in the control of body temperature. But why should the older goal of causing body temperature to oscillate have been retained during evolution? A possible reason to retain rhythmicity of body temperature in homeotherms is the ability to use body temperature

as an internal non-photoc zeitgeber for the entrainment of multiple slave pacemakers distributed throughout the body [665–671]. Presumably, environmental light affects the master circadian pacemaker in the brain, which modulates the body temperature rhythm (through behavioral mechanisms in ectotherms and through behavioral and autonomic mechanisms in endotherms), which then non-photically modulates the peripheral clocks. Alternatively, the presence of a circadian rhythm of body temperature in extant homeothermic species may simply reflect the preservation of the body temperature rhythm as a vestigial function in animal evolution.

Regardless of whether the generation of the body temperature rhythm is a fundamental process or not, one can still wonder how the rhythm is produced. How does the circadian system generate the circadian rhythm of body temperature? The laws of thermodynamics require that changes in the temperature of a body be the result of changes in heat flow. Changes in body temperature must result from the balance of heat gained and heat lost. For mammals and birds housed in a thermally stable environment without direct solar radiation, heat is gained by metabolic heat production, and heat is lost by radiation, conduction, and convection [17–19]. Few studies have included the simultaneous recording of body temperature, heat production, and heat loss, but one example is presented in Figure 8. Shown are 3-day segments of the records of body temperature, metabolic heat production, and dry heat loss of a laboratory rat kept in constant darkness at an ambient temperature of 24°C [612]. Notice that the oscillation of body temperature parallels the oscillation of heat production. Thus, the oscillation of heat production could potentially explain the oscillation of body temperature. However, notice also that heat loss parallels heat production. That is, although heat production is high when body temperature is high, heat loss is also high. This apparent paradox results from an incorrect assumption that a great amount of heat is needed to generate the body temperature rhythm. In reality, most of the energy expenditure of, say, a rat is associated with essential life processes, the maintenance of homeothermy, and energy required for locomotion. The body temperature rhythm accounts for only about 6% of the energy expended at thermoneutrality

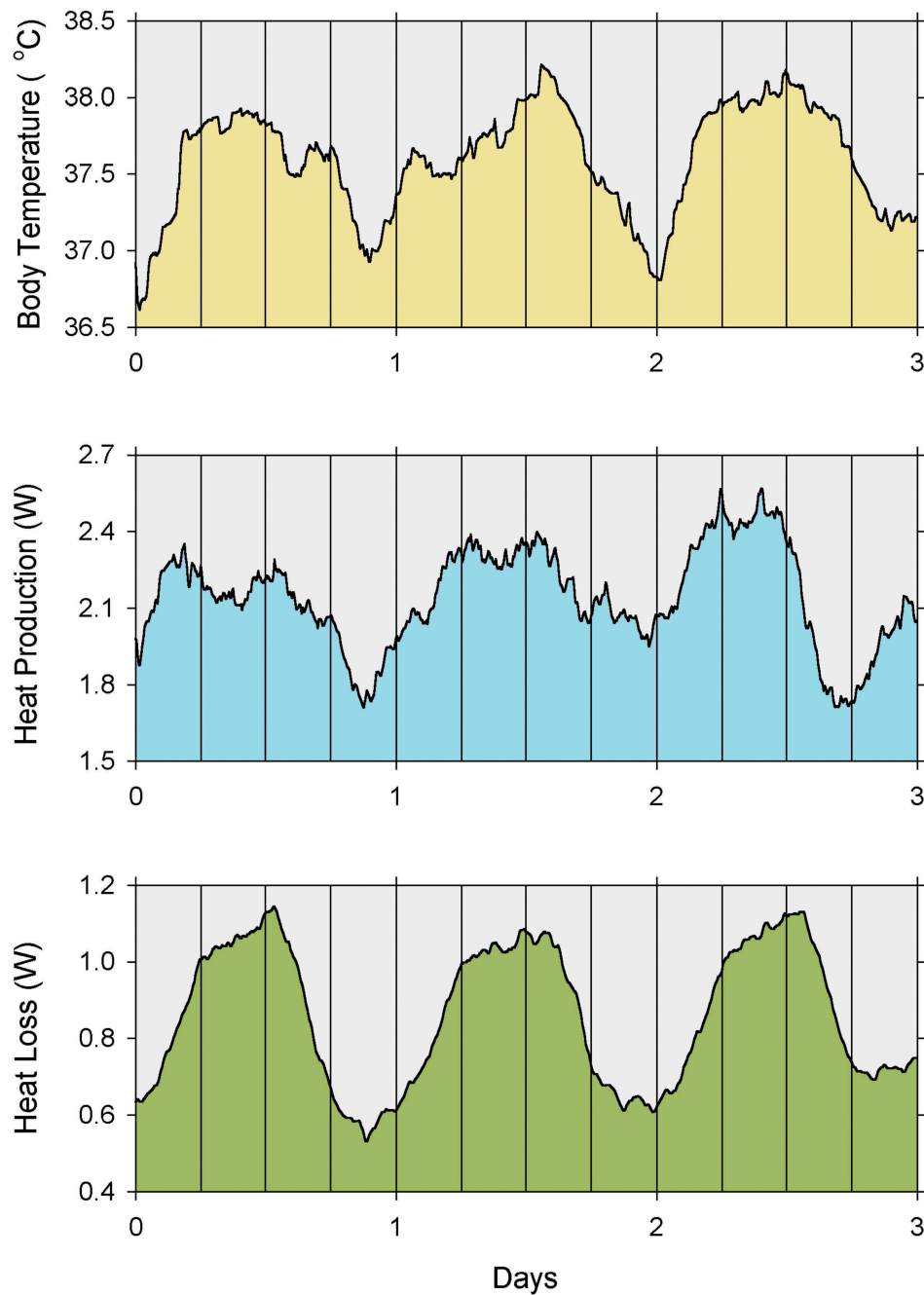
and only 3% of the energy expended in the cold [612,672]. Thus, most of the daily oscillation in heat production and heat loss has nothing to do with the body temperature rhythm. The mechanism responsible for the circadian rhythm of body temperature is a minor temporal mismatch between heat production and heat loss, which causes the small change in heat balance needed to generate the body temperature rhythm [612].

### Relationship of circadian rhythmicity and metabolism at the cellular level

After having discussed the relationship of body temperature and metabolism at the organismal level, it would seem reasonable to discuss the same relationship at the cellular level. However, individual cells do not regulate their own temperature. Body temperature regulation is an organismal process. In fact, the circadian clock is temperature compensated and need not make adjustments for changes in temperature [673–675], even if other cellular processes are subject to temperature-induced variations in the rate of chemical reactions dictated by the Arrhenius equation. On the other hand, individual cells do possess circadian clocks, and the relationship of circadian rhythmicity and metabolism can be discussed at the cellular level.

It has been known for over 20 years that the molecular mechanism of the circadian clock in animals involves an auto-regulatory transcriptional feedback loop in which the proteins Clock and Bmal1 activate the transcription of the *period* and *cryptochrome* genes. The Period and Cryptochrome proteins then feed back and repress their own transcription by interaction with Clock and Bmal1 [676,677]. This is the backbone of the clock itself, but much has yet to be learned about how enzyme transcripts controlled by the clock generate circadian enzyme activity [678]. One research group has found that the circadian clock generates oscillations in mitochondrial oxidative capacity via rhythmic regulation of NAD<sup>+</sup> biosynthesis [679], as diagrammed in Figure 9.

It was suggested early on that metabolism might be more than just an output of the clock and might actually be part of the clock [680]. Research conducted during the past 20 years indicates that, indeed, metabolism is both an output from and an input to the circadian

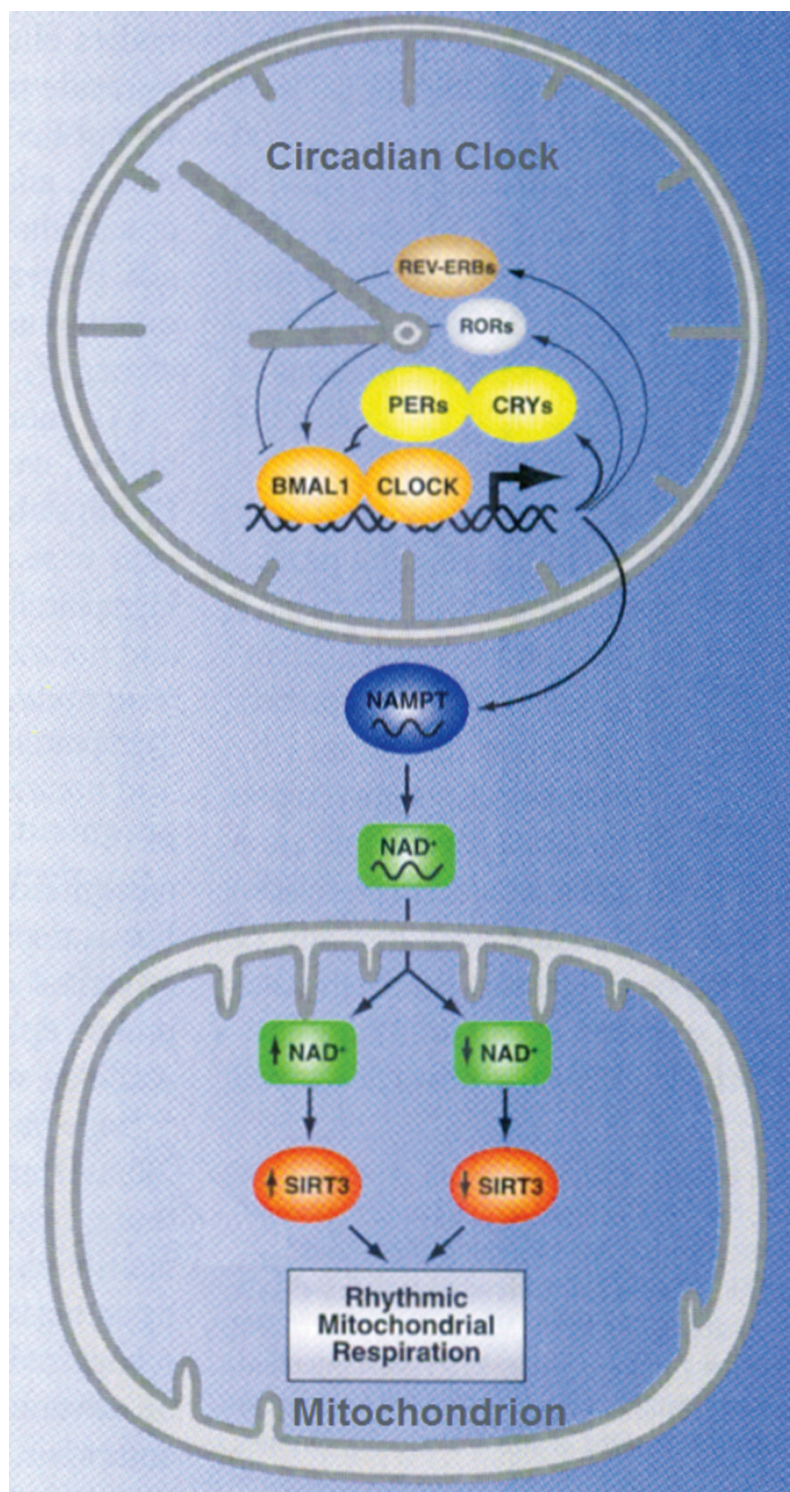


**Figure 8.** Records of body core temperature, metabolic heat production, and dry heat loss of a laboratory rat kept in constant darkness at an ambient temperature of 24°C for three consecutive days. The data were collected and are plotted with 6-minute resolution after smoothing by a 4 hour moving averages filter to eliminate high-frequency oscillations.

clock [522,681,682], meaning that the two processes are interlinked. One example is the protein Conidial Separation Protein 1 (CSP-1) in the bread-mold fungus *Neurospora crassa* [683]. In *Neurospora*, the transcriptional feedback loop of the circadian clock organizes the molecular output of the cell so that catabolic processes occur in the morning and anabolic processes

occur in the evening. The *csp-1* gene is directly targeted by the clock (which in *Neurospora* is composed primarily of the *wc1-wc2* and *frq* genes). Interestingly, CSP-1 acts to compensate the clock for changes in metabolic conditions. Specifically, CSP-1 is regulated by glucose levels and represses the expression of *wc-1* mRNA when glucose levels are high [683].





**Figure 9.** Diagram of the cellular mechanism of circadian regulation of metabolism in the mouse. From Peek and colleagues [679]. Reprinted with permission from AAAS.

A major unanswered question is, of course, how circadian rhythmicity of metabolism at the cellular level relates to circadian rhythmicity at the organismal level, particularly in complex organisms such as birds and mammals.

## Conclusion

Published studies clearly document circadian rhythmicity of body temperature and metabolism. The rhythms of both variables are generated endogenously



in birds and mammals, are synchronized with the Earth's rotation by environmental cycles, and are further modulated by occasional and recurrent events in the environment, particularly variations in ambient temperature and food availability. Although modulation of metabolic heat production is a constitutive process of the body temperature rhythm, the rhythm of body temperature is not produced by the rhythm of heat production associated with physical activity and sleep-wakefulness. The body temperature rhythm is achieved by a small variation in heat balance that results from a minor temporal mismatch between heat production and heat loss. At the cellular level, the circadian clock and metabolism are deeply intertwined, although it is still not clear how this intertwining is reflected at the organismal level.

## Disclosure statement

The author reports no conflicts of interest.

## Notes on contributor



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